

## A CLADISTIC REASSESSMENT OF OCTOPODID CLASSIFICATION

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### ABSTRACT

Octopodid classifications have been traditionally, and are currently, based on a few readily apparent characters. In this analysis, I examine methods that have contributed to octopodid classifications from a cladistic perspective that emphasizes the recognition of monophyletic groups, and I apply parsimony algorithms to the data set reported by Voss (1988a) for the Octopodidae. I reject current and previous subfamily classifications of the Octopodidae as having created paraphyletic groups. Use of the category subfamily should be avoided, as it implies our knowledge of octopodid evolution has reached level that is as yet unattained.

To further our knowledge of octopod phylogeny, we must define primitive and derived characters states by objective criteria, consider only monophyletic species groups in our analyses and expand the range of characters considered. Analysis of the data set compiled for cladistic analysis reveals that characters of the radula, anterior digestive system and skin change in concert. These associated character changes may indicate underlying functional relationships that have been unsuspected.

Key words: Octopodidae, parsimony analysis, Graneledoninae, Eledoninae, Bathypolypodiinae, Octopodinae, systematics, radula.

### INTRODUCTION

Taxonomic treatments intended to identify astonishingly different, or to separate overtly similar, specimens have produced the current classification of coleoid cephalopods. This scheme, similar to Naef's (1923) reconstruction of ancestor-descendent relationships, groups taxa based on morphological similarity, with primitive characters contributing as much as derived characters. That comparatively few characters support subfamily groups in octopodids have been cited as evidence of the family's chaotic evolution (Robson, 1932). Whether these formally recognized morphologically distinct groups constitute monophyletic lineages that share a common evolutionary history is unknown.

Phylogenetic reconstruction through phylogenetic or cladistic analysis seeks to recognize only monophyletic groups. The possession of shared derived characters (synapomorphies) is the criterion on which monophyletic groups are recognized. Neither shared primitive characters (symplesiomorphies) nor character states unique to a single taxon (autapomorphies) provide information concerning relationships.

Cladistic analysis considers as many presumed synapomorphies as possible. Homoplasy (whether due to parallelism, convergence or reversal) affects some character changes, but these are assumed to be fewer

than the character changes that reflect unique modification with descent from a common ancestor. Cladistics uses the absolute criterion of parsimony to evaluate alternate hypotheses of relationships; parsimony dictates that the hypothesized relationship that requires the fewest number of character changes is the most likely to reflect history.

In this paper, I test the extent to which octopodid classification is supported by cladistic analysis. I apply parsimony analysis to the characters reported by Voss (1988a). My intent is to introduce a cladistic perspective to octopodid systematics, to examine implicit assumptions that may have affected earlier treatments of the group and to assess the information contained in traditional characters.

### THE OCTOPODS

Among octopods, the bathypelagic taxa of the suborder Cirrata are unified by the presence of fins, cirri and internal shells, all primitive characters (Naef, 1923; Robson, 1932; Voss, 1988a). Members of the suborder Incirrata, which occur throughout the water column and in benthic habitats, are united by the absence of these characters, and by egg care by the female, and associated characters (Boletzky, 1992). Among the incirrates, male reproductive characters and pelagic habitats

TABLE 1. Octopodid classifications of Grimpe (1921, 1922), Robson (1932), Thiele (1934) and Voss (1988a). Listed are the subfamilies and their diagnostic characters; in addition to these characters, geographic and depth distribution are also cited in subfamily definitions.

Reference	Subfamilies	Sucker rows	Ink sac	Other characters
Grimpe (1921, 1922)	Octopodinae	2	±	small eggs
	Eledoninae	1 or 2	±	large eggs
Robson (1932)	Octopodinae	1 or 2	±	typical
	Bathypolypodinae	1 or 2	—	reduced crop, gills, radula; large eggs, spermatophores, squat body; double funnel organ; narrow mantle aperture
Thiele (1934)	Octopodinae	1 or 2	+	generally small eggs
	Bathypolypodinae*	1 or 2	—	reduced crop; large eggs & spermatophores; short arms; narrow mantle aperture
Voss (1988a)	Ozaeninae (Eledoninae)	1	+	large eggs
	Octopodinae	2	+	
	Bathypolypodinae	2	—	
	Eledoninae	1	+	
	Graneledoninae	1	—	

\*Including *Benthoctopus* and *Teretocopus*, despite the large crop of *Teretocopus*.

define membership in the argonauts; multicupid radular teeth and adaptation to the mesopelagic zone define members of the Ctenoglossa. The Octopodidae, with the most recognized species, contains the benthic octopuses. Prominent among the few characters that have contributed to octopodid classification (Table 1) are the number of sucker rows and the presence or absence of an ink sac.

Members of the Octopodidae range from the intertidal zone to over 3500 m depth and from the equator to the polar ice caps (Voss, 1988b). I follow taxonomic tradition in assuming that the Octopodidae represent a monophyletic group. Although Naef (1923) suggested the pelagic Argonautida are derived from *Octopus s. s.*, I assume here that the characters cited as uniting these groups (e.g. double sucker rows, ink sac) are better attributed to convergences and symplesiomorphies than to synapomorphies (Robson, 1932; Voight, 1990).

Based on similarities in their radulae, the monotypic taxon, *Vitreledonella*, has been suggested to be an octopodid derived for the mesopelagic habitat (Robson, 1932). Although *Vitreledonella* lacks the multicupidate radula that has defined the Ctenoglossa (an apparent clade of the meso- and bathypelagic octopods), this taxon and the ctenoglossid *Amphetrurus* share a rotated digestive

system unique in the Cephalopoda (Thore, 1949). I tentatively consider *Vitreledonella* to be a ctenoglossid (Voight, 1990) and exclude it from this analysis.

## METHODS

Taxa that serve as the operational taxonomic units (OTUs) in this analysis are octopodid genera. Genera that Toll (1991) recently revitalized are not included, pending complete diagnoses. The characters Voss (1988a) cited as diagnosing nonoctopodine genera and his polarity assessments are summarized on Table 2. For genera not included by Voss (1988a), data were gathered from specimens and literature accounts. Octopodine genera other than *Scaergus* and *Pteroctopus* (i.e., *Robsonella*, *Hapalochlaena*, *Cistopus*, *Enteroctopus*, *Euaxoctopus*), however, do not differ from *Octopus* in the characters considered (Robson, 1929; Roper & Hochberg, 1988; Hochberg et al., 1992). These taxa were excluded, as autapomorphies cannot contribute to the analysis.

The data matrix (Appendix 1) was analyzed by PAUP (Version 3.0) using subtree pruning-regrafting and the MULPARS option (Swofford, 1989). The specified ancestor (Appendix 1) served to root the analysis. Characters with polarities defined by Voss (1988a; Table 2)

TABLE 2. Characters, character state definitions, and stated reasoning behind polarity definitions (Voss, 1988a).

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0 = ancestral character state; 1 = derived state.

1. Number of sucker rows: 0 = one; 1 = two (after Naef).
2. Ink sac: 0 = present; 1 = absent (known in fossil cephalopods).
3. Crop: 0 = with diverticulum; 1 = with dilation. (Loss of diverticulum is a modification to small prey.)
4. Posterior salivary glands: 0 = large; 1 = small; 2 = vestigial. (Large is normal in shallow-water forms.)
5. Rachidian lateral cusps: 0 = present; 1 = absent (commonality).
6. Lateral tooth: 0 = present; 1 = absent (commonality).
7. Marginal plates: 0 = present; 1 = absent (commonality).
- 8, 9. Funnel organ: 00 = W-shaped; 01 = VV; 10 = IIII (commonality).
10. Gill lamellae per demibranch: 0 = 9 or more; 1 = less than 9.  
(Reduction assumed to be adaptive in the deep sea.)
11. Egg length: 0 = less than 11 mm; 1 = 12–13 mm; 2 = over 15 mm (polarity rationale unclear).
12. Spermatophore size: 0 = small; 1 = medium; 2 = large (commonality, also small in cirrates).
13. Mantle aperture width: 0 = narrow (A or B); 1 = wide (C) (polarity rationale unclear).
14. Skin texture: 0 = smooth; 1 = papillose; 2 = tubercles (polarity rationale unclear).
15. Supra-ocular cirri: 0 = absent; 1 = present (polarity rationale unclear).

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were entered as ordered; characters with uncertain polarities (egg length, mantle aperture width, skin texture, supra-ocular cirri; Table 2) were entered unordered.

States of functionally related characters were examined to assess whether characters changed independently, or in concert. If associated changes were identified, characters were recoded as a single, multistate character.

## RESULTS

Analysis of the data set (Appendix 1) resulted in at least 1999 equally parsimonious trees (35 steps, consistency index 0.514). The strict consensus tree, which depicts groups supported by all equally parsimonious trees, revealed two groups, one containing *Pareledone*, *Eledone*, *Octopus*, *Benthoctopus* and *Teretotopus*, and the other containing the remaining nine genera. None of the 1999 equally parsimonious topologies (Fig. 2) are consistent with Voss' evolutionary tree (Fig. 1). Voss' tree, when analyzed by cladistic methods requires 49 steps, i.e. 14 steps (40%) more than the most parsimonious solution.

Relaxation of the strict consensus constraint illustrates relationships supported by some (in this case by at least 60%) but not all, of the alternate trees (majority rule consensus  $n = 60\%$ ). *Bathypolypus* is suggested to be more closely related to *Graneledone*, *Thaumeledone* and *Bentheledone* than to any taxon with which it shares biserial suckers. Of

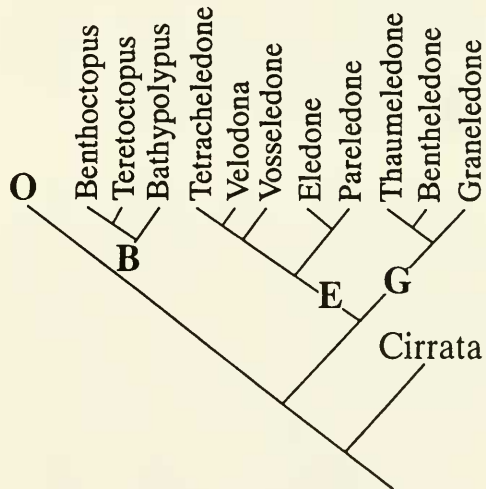


FIG. 1. The evolutionary tree presenting subfamily and generic relationships of the benthic Octopodidae, rooted to the Cirrata, excluding oceanic forms (after Voss 1988a: 274). O, Octopodinae; B, Bathypolypodinae; E, Eledoninae; G, Graneledoninae.

Voss' generic relationships (Fig. 1), close relationships between *Benthoctopus*-*Teretotopus* and *Thaumeledone*-*Bentheledone* are supported at the indicated levels. The strict consensus tree requires the number of sucker rows to change and the ink sac to be lost at least twice. The majority rule consensus arrangement requires these changes, and an additional change in the number of sucker rows.

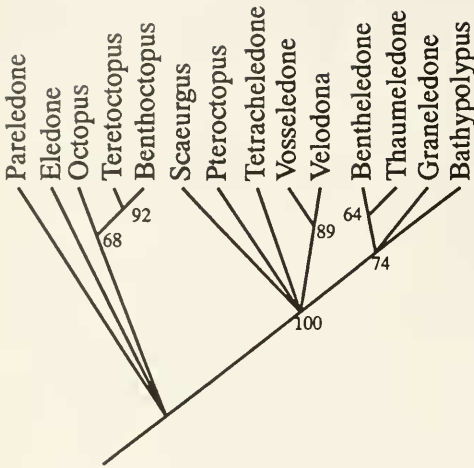


FIG. 2. Diagrammatic results of the cladistic analysis of data set in Appendix 1, rooted to the hypothetical ancestor. Numbers at the nodes indicate the proportion of the 1999 equally parsimonious trees discovered that support that node. The node indicated by 100 is the limit of resolution supported by all equally parsimonious trees.

Examination of the data matrix (Appendix 1) reveals that several functionally related characters change in concert. All taxa that lack marginal plates (character 7) also lack lateral teeth (character 6); all taxa that lack lateral teeth also have a homodont rachidian (character 5). These changes in the radula appear to occur in a cascade pattern. A similar suite of changes is also seen in the anterior digestive system (no taxon with small posterior salivary glands, character 5, has a crop diverticulum, character 4) and between skin texture and supraocular cirri (characters 14, 15). Recoding associated characters as single multistate characters maintains the information in the original data matrix, reflects the associated nature of the changes and condenses the number of characters from 15 to 11 (Appendix 2).

## DISCUSSION

Cladistic analysis (Fig. 2) of characters traditionally used in octopodid classification indicates that the octopodid subfamilies are, and have been, paraphyletic (Table 1). Although these subfamilies have been defined on comparatively obvious differences, they

cannot be held to share evolutionary histories.

The uncertain status of octopodid subfamilies has been a subject of earlier discussion. In Robson's original (1928) definition, the Bathypolypodinae (two sucker rows and no ink sac) included *Bathypolypus*, *Benthooctopus* and *Teretoctopus*. In 1932, Robson redefined the group (Table 1) to include *Bathypolypus*, *Graneledone*, *Thaumeledone* and *Benteledone*, with *Benthooctopus* and *Teretoctopus* assigned to the Octopodinae. Robson (1932: 49–56) apparently recognized that, although his original definition of Bathypolypodinae created a morphologically distinctive and cohesive group, the presence of multiple characters refuted monophyly of the Eledoninae and a close relationship between *Bathypolypus* and *Benthooctopus*.

Robson stated that his (1932) definition of the Bathypolypodinae may have made the Octopodinae paraphyletic; Figure 2 supports this suggestion. Because *Scaeurgus*, *Pterooctopus*, *Tetracheledone*, *Vosseledone* and *Velodona* appear to share a more recent common ancestor with members of the Bathypolypodinae than do *Pareledone*, *Eleledone*, *Octopus*, *Teretoctopus* or *Benthooctopus* (Fig. 2), including them in the Octopodinae creates an unnatural group that exists only in the classification. Voss (1988a), rejected Robson's subfamilies, in essence, to return to those erected earlier.

As we appear to be unable to define subfamilies that are even arguably monophyletic, use of the taxonomic category of subfamily should be avoided. The presence of an artificial category implies a level of knowledge that we have yet to achieve; in doing so, it impedes the discovery of evolutionary histories. Octopodid groups may best be defined for discussion by ecological or ontogenetic criteria, for example, holobenthic (Boletzky, 1992).

Among the major problems octopod systematics faces is how to define ancestral states. In this analysis, the definition of the hypothetical ancestor as nearly identical to shallow-water taxa ensures that deep water taxa will be found to be derived. This traditional view (Naef, 1923; Robson, 1925, 1932; Voss, 1967) may be an artifact of the taxonomic need to distinguish comparatively rare specimens of deep water taxa from familiar, normal octopuses.

That the common ancestor of the incirrate octopods was a benthic octopod, based on

the rationale that the loss of the fins would not be adaptive in pelagic forms (Boletzky, 1992), has canalized the way we think of the group. Young (1977) attributed the absence of the supra-brachial commissure in the ctenoglossan *Japetella* to loss associated with adaptation to a pelagic habitat from a benthic ancestral state. In that evolutionary scenario, the possibility that the suprabrachial commissure is a synapomorphy shared by octopodids and argonauts is eliminated from consideration.

To ensure alternate octopodid relationships are considered, primitive states must be defined by objective criteria such as outgroup analysis or ontogeny (see discussion by Bryant, 1991). Whether a given character state is widely distributed, occurs in the most common species, or characterizes the most diverse taxon, does not demonstrate that it is ancestral.

Systematic studies of octopodids are also hindered by our inability to define monophyletic species groups. Taxonomy succeeds if specimens can be assigned to genera; systematics fails if genera do not share a common history. Members of the genus *Pareledone*, for instance, are separable from those of *Eledone* and *Graneledone*. Whether they represent divergent octopodid lineages that lack the diagnostic synapomorphies, or are united by a unique history is unknown and cannot be discovered with the available characters. The taxon Eledoninae of Voss (1988a), and the genus *Octopus* itself are affected by the same problem. These taxa are the leftovers after the removal of those with synapomorphies. Incorrectly assuming monophyly for species groups obscures patterns of character change, and can undermine the analysis.

Too few characters of uncertain (or untested) homology also limit phylogenetic reconstruction of the octopodids. Characters of loss and reduction dominate this data set. Although Begle (1991) showed reductive characters to be as informative as character gains, and Voss & Voss (1983) found losses as informative as gains in their cladistic analysis of the cranchiid squids, in this analysis too few positive characters are available to test this statement. Perhaps because taxonomy has focused on differences between deep-sea and shallow-water octopuses, several of the characters used here (e.g. ink sac, crop, posterior salivary glands, gill lamellae, egg size, mantle aperture) are losses and reductions that may be under direct selection in

deep-water habitats (Robson 1925, 1932; Voss, 1967, 1988a).

Every opportunity must be used to increase our knowledge of octopod biology. Because cladistic analysis requires explicit definition of the characters and character states considered in the analysis, the data set documents associated change in characters (Appendices 1, 2). The presence of associated change may indicate the existence of a functional relationship among characters that might otherwise be undetected; it can provide insight into the biology of the animals.

The radular reductions among the octopodids that have been viewed as independent (characters 5–7, Appendix 1) show unexpectedly orderly character change (Appendix 2). Only taxa in which the rachidian is homodont lose the first lateral tooth; only taxa without the first lateral teeth lose the marginal plates. This sequence suggests that the radulae of taxa with homodont rachidians differ functionally from those with a multicuspid rachidian, in which the radular teeth may function as a mutually supporting bracing mechanism (Solem & Roper, 1975). Similar changes in the digestive system, that only taxa without a crop diverticulum have small posterior salivary glands, suggest that these taxa allocate digestive enzymes differently. The changes appear to be neither independent nor random, although we must demonstrate that they are functionally associated. Defining each of these conditions as separate inflates the number of characters without increasing the information entered into the analysis. Eleven characters cannot resolve relationships among 14 taxa.

It may be argued that these data were not intended for parsimony-based methodology, and that cladistic analysis violates the premise and rationale behind their collections and initial analyses. Other, undocumented characters may have contributed to the recognition of these taxonomic groups. Group definitions relying on subtle, inexpressible similarities, however, only further support that morphological cohesiveness defines the groups. Explicit reliance on these few characters, and on paraphyletic groups they have created, has limited our knowledge of octopod evolution. We must recognize and eliminate artificial taxonomic divisions to begin modern systematic treatments of this cosmopolitan marine group. Shedding preconceived notions may free us to discover the monophyletic groups that evolution has produced.

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## LITERATURE CITED

- BEGLE, D. P., 1991, Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. *Systematic Zoology*, 40: 33–53.
- BOLETZKY, S. v., 1992, Evolutionary aspects of development, life style, and reproductive mode in incirrate octopods (Mollusca, Cephalopoda). *Revue Suisse Zoologie*, 99: 755–770.
- BRYANT, H. N., 1991, The polarization of character transformations in phylogenetic systematics: role of axiomatic and auxiliary assumptions. *Systematic Zoology*, 40: 433–445.
- GRIMPE, G., 1921, 2. Teuthologische Mitteilungen. VII. Systematische Übersicht der Nordseecephalopoden. *Zoologischer Anzeiger*, 52: 296–304.
- GRIMPE, G., 1922, Systematische Übersicht der europäischen Cephalopoden. *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig*, 9: 36–52.
- HOCHBERG, F. G., M. NIXON & R. B. TOLL, 1992, Order Octopoda Leach, 1818. Pp. 213–279, in: M. J. SWEENEY, C. F. E. ROPER, K. M. MANGOLD, M. R. CLARKE & S. v. BOLETZKY, eds., "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513.
- NAEF, A., 1923, *Cephalopoda*. Part I, Vol. I, Fascicle II, in *Fauna and Flora of the Bay of Naples*, 35. Israel Program for Scientific Translations, Jerusalem, pp. 293–879.
- ROBSON, G. C., 1925, The deep sea Octopoda. *Proceedings of the Zoological Society of London*, 1925: 1323–1356.
- ROBSON, G. C., 1928, Notes on the Cephalopoda. VI. On *Grimpella*, a new genus of Octopoda, with remarks on the classification of the Octopodidae. *Annals and Magazine of Natural History*, (10)2: 108–114.
- ROBSON, G. C., 1929, *A monograph of the Recent Cephalopoda. Part 1. The Octopodinae*. British Museum of Natural History, 236 pp.
- ROBSON, G. C., 1932, *A monograph of the Recent Cephalopoda. Part 2. Octopodidae exclusive of the Octopodinae*. British Museum of Natural History, 359 pp.
- ROPER, C. F. E. & F. G. HOCHBERG, 1988, Behavior and systematics of cephalopods from Lizard Island, Australia, based on color and body patterns. *Malacologia*, 29: 153–193.
- SOLEM, A. & C. F. E. ROPER, 1975, Structures of recent cephalopod radulae. *The Veliger*, 18: 127–133.
- SWOFFORD, D. L., 1989, *PAUP phylogenetic analysis using parsimony*. III. Natural History Survey, Champaign, Ill.
- THIELE, J., 1934, *Handbuch der systematischen Weichtierkunde*. Verlag von Gustav Fischer, Jena, 3: 779–1022 pp.
- THORE, S., 1949, Investigations of the "Dana" Octopoda. Part I. Bolitaenidae, Amphitretidae, Vitreledonellidae, and Alloposidae. *Dana Report*, 33: 1–85.
- TOLL, R. B., 1991, The supraspecific classification of the Octopodinae (Cephalopoda: Octopoda): a review. *Bulletin of Marine Science*, 49: 668.
- VOIGHT, J. R., 1990, *Population biology of Octopus digneti and the morphology of tropical American octopuses*. Ph.D. Dissertation, University of Arizona, Tucson, 196 pp.
- VOSS, G. L., 1967, The biology and bathymetric distribution of deep-sea cephalopods. *Studies in Tropical Oceanography*, 5: 511–535.
- VOSS, G. L., 1988a, Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). Pp. 253–276, in: M. R. CLARKE & E. R. TRUEMAN, eds., *The Mollusca Vol. 12. Paleontology and neontology of cephalopods*, Academic Press, San Diego.
- VOSS, G. L., 1988b, The biogeography of the deep-sea Octopoda. *Malacologia*, 29: 295–307.
- VOSS, N. A. & R. S. VOSS, 1983, Phylogenetic relationships in the cephalopod family Cranchiidae (Oegopsida). *Malacologia*, 23: 397–426.
- YOUNG, J. Z., 1977, Brain, behaviour and evolution of cephalopods. *Symposium of the Zoological Society of London*, 38: 377–434.

APPENDIX 1. Reported are the data matrix, including for each OTU, characters coded as indicated on Table 2 (9 = character absent, or polymorphic within genus), the total number of characters coded as derived and the estimated mean depth distribution of each genus (Voss, 1988b).

OTU	CHARACTER NUMBER															Σ	Depth	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5			
ANCESTOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OCTOPUS	1	0	0	0	0	0	0	0	0	0	9	0	0	0	0	1	46	
ELEDONE	0	0	0	0	0	0	0	0	9	0	9	0	9	1	0	1	157	
PARELEDONE	0	0	0	0	0	0	0	0	9	0	0	0	9	9	0	0	481	
TERETOCTOPUS	1	1	0	9	0	0	0	1	0	0	9	9	9	0	0	4	907	
BENTHOCTOPUS	1	1	0	0	0	0	0	0	9	0	1	9	0	0	0	3	1060	
SCAEURGUS	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	4	275	
TETRACHELEDONE	0	0	0	0	1	0	0	1	0	1	0	1	0	2	1	6	364	
PTEROCTOPUS	1	0	1	1	0	0	0	0	1	0	0	0	9	1	1	6	410	
VOSELEDONE	0	0	0	0	1	1	1	0	1	1	1	1	1	1	9	9	105	
VELODONA	0	9	0	0	1	0	0	0	1	0	9	1	1	2	1	6	588	
GRANELEDONE	0	1	1	1	9	9	0	0	1	1	1	2	0	2	1	9	1721	
BATHYPOLYPUS	1	1	1	1	1	0	0	0	1	1	0	2	0	1	1	10	790	
THAUMELEDONE	0	1	1	2	1	1	0	0	1	1	0	2	0	1	0	9	1388	
BENTHELEDONE	0	1	1	2	1	1	1	0	1	1	1	2	0	1	9	11	3354	

APPENDIX 2. Data matrix recoded to reflect associated (cascading) changes in character states, and thus the reduction in the number of characters from 15 to 11. Characters defined as in Table 1, except 3, 5 and 14, below.

OTU	CHARACTER NUMBER												
	1	2	3*	5*	8	9	0	1	1	1	1	1	4*
OCTOPUS	1	0	0	0	0	0	0	0	9	0	0	0	0
ELEDONE	0	0	0	0	0	0	9	0	9	0	0	9	1
PARELEDONE	0	0	0	0	0	0	9	0	0	0	0	9	9
TERETOCTOPUS	1	1	0	0	1	0	0	0	9	9	9	9	0
BENTHOCTOPUS	1	1	0	0	0	0	9	0	1	9	0	0	0
SCAEURGUS	1	0	0	0	0	0	0	0	0	1	0	2	2
TETRACHELEDONE	0	0	0	1	1	0	1	0	1	0	3	3	3
PTEROCTOPUS	1	0	1	0	0	1	0	0	0	0	9	2	2
VOSELEDONE	0	0	0	3	0	1	1	1	1	1	1	1	1
VELODONA	0	9	0	1	0	1	0	9	1	1	3	3	3
GRANELEDONE	0	1	1	9	0	1	1	1	2	0	3	3	3
BATHYPOLYPUS	1	1	1	1	0	1	1	0	2	0	2	2	2
THAUMELEDONE	0	1	2	2	0	1	1	0	2	0	1	1	1
BENTHELEDONE	0	1	2	3	0	1	1	1	2	0	1	1	1

3\*. 0 = crop diverticulum; 1 = crop dilation; 2 = crop dilation and posterior salivary gland reduction.

5\*. 0 = radula with 7 teeth; rachidian multicuspid; 1 = radula with 7 teeth, rachidian non-cuspid; 2 = rachidian non-cuspid and lateral teeth absent, 3 = rachidian non-cuspid, lateral teeth and marginal plates absent.

14\*. 0 = smooth skin; 1 = papillose skin; 2 = papillose skin with supra-ocular cirri; 3 = tubercles and supra-ocular cirri.